

# Bats respond to polarity of a magnetic field

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Bats have been shown to use information from the Earth's magnetic field during orientation. However, the mechanism underlying this ability remains unknown. In this study we investigated whether bats possess a polarity- or inclination-based compass that could be used in orientation. We monitored the hanging position of adult *Nyctalus plancyi* in the laboratory in the presence of an induced magnetic field of twice Earth-strength. When under the influence of a normally aligned induced field the bats showed a significant preference for hanging at the northern end of their roosting basket. When the vertical component of the field was reversed, the bats remained at the northern end of the basket. However, when the horizontal component of the field was reversed, the bats changed their positions and hung at the southern end of the basket. Based on these results, we conclude that *N. plancyi*, unlike all other non-mammalian vertebrates tested to date, uses a polarity-based compass during orientation in the roost, and that the same compass is also likely to underlie bats' long-distance navigation abilities.

**Keywords:** *Nyctalus plancyi*; orientation; polarity compass; hanging position

## 1. INTRODUCTION

Intensity and direction of the Earth's magnetic field are considered to be omnipresent and reliable sources of navigational information for animals. The vector component of the field can provide directional information and inclination or total intensity can be used to indicate position (Wiltschko & Wiltschko 2005). Many animals, including amphibians, fishes, birds, mammals and a variety of invertebrates, have been shown to use a magnetic compass during orientation (Wiltschko & Wiltschko 1995, 2005). Within the mammals, rodents have been shown to use magnetic field information during orientation, navigation and nesting (Mather & Baker 1981; Deutschlander *et al.* 2003; Kimchi *et al.* 2004; Muheim *et al.* 2006), while bats have recently been shown to use it during orientation (Holland *et al.* 2006). In all non-mammalian vertebrates tested to date, the inclination of the magnetic field is used to determine the direction of the field (Phillips & Borland 1994; Wiltschko & Wiltschko 1996, 2005; Walker *et al.* 2002). In contrast, mole rats, the only mammal in which directional orientation has been analysed in detail, use the polarity of the field to determine direction (Marhold *et al.* 1997).

As the second most abundant order of mammals, bats have been shown to use vision, olfaction and echolocation for orientation and short-range navigation between roosts and foraging sites (Altringham 1998). Although bats displaced outside their home ranges have also recently been shown to use the magnetic field during orientation (Holland *et al.* 2006), it remains unknown whether they

use magnetic polarity or inclination to determine the direction. In this paper we test the null hypothesis that bats are unable to detect the changes in the polarity and inclination of an induced magnetic field. To test our hypothesis, we exposed individuals of the species *Nyctalus plancyi* (Chiroptera: Vespertilionidae), held in a laboratory, to an induced magnetic field of twice Earth-strength. We then altered, both simultaneously and independently, the horizontal and vertical components of the field and monitored the effects on the roosting behaviour of the bats. Reaction to changes in the vertical field would demonstrate sensitivity to the inclination of the field, while reaction to changes in the horizontal field would demonstrate sensitivity to the polarity of the field.

## 2. MATERIAL AND METHODS

### (a) Test bats

The study was carried out in two phases: from 13 November 2005 to 21 January 2006 and from 12 July 2006 to 1 May 2007. All bats used in this study were captured from the Dule Temple (40°5' N, 117.4° E) in Tianjin Province, approximately 100 km east of Beijing, in September 2005 and July 2006. All bats were released back into the wild following their use in our experiments. The bats were fed with mealworms, supplemented with vitamins and fresh water each night.

### (b) Test conditions

All trials were carried out at Beijing, in a controlled temperature laboratory to prevent bats entering torpor or hibernation. Bats were simultaneously placed into an inverted plastic round basket (30 cm in diameter) with holes in the sides, which allowed the bats to climb and hang from the base of the basket after it was turned upside down. The basket was

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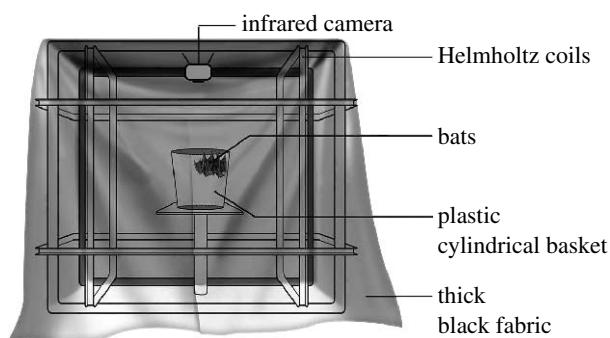


Figure 1. Experimental chamber in which the bats were exposed to the altered magnetic field.

placed in the test chamber at the centre of three orthogonally aligned, independently controlled square Helmholtz coils ( $D=1.5$  m). The coils were covered with thick black fabric to isolate the bats from external light sources (figure 1). The laboratory was free from visual, olfactory and acoustic cues, which the bats could use as a reference point.

**Olfaction:** the roosting basket was cleaned carefully with fresh water and alcohol each night while the bats were taken away for feeding. **Illumination and sound:** the Helmholtz coils were covered with thick black fabric. Inside the cover it was completely dark with a light intensity less than 0.03 lux during the experiment period (tested using a digital light meter, TES-1330A, TES Electrical Electronic Corporation Taipei, Taiwan), and the sound intensity was less than 35.0 dB (TES-1350A, range 35–100 dB  $\pm$  2 dB between 31.5 Hz and 8 kHz). **Temperature and humidity:** temperature and relative humidity were monitored over the course of the experiments; fluctuation was less than 9% (temperature and humidity meter THG312, Oregon Scientific, Portland, Oregon).

Levels of background sound, light, temperature and humidity were equal in all directions around the basket. Each evening the bats were removed from the basket, fed and then returned to the basket for testing.

### (c) Local geomagnetic field

The geomagnetic field in Beijing at the time of experiments was: declination =  $353.7^\circ$ , inclination =  $58^\circ$  and intensity  $H=54.5$   $\mu$ T.

### (d) Data analysis

Each day (16.00) we recorded the hanging position of the bats via an infrared camera. The bats' mean roosting position was calculated from the hanging position of the cluster of bats. We recorded one mean position per day for each phase. A mean vector with the direction  $\alpha$  was calculated based on the positions, and the mean vectors were tested for non-uniformity using the Rayleigh test. The differences in average vectors when bats were subjected to normal and reversed fields were tested using the Watson  $U^2$ -test (Zar 1974).

## 3. RESULTS

In baseline experiments, six wild adult *N. plancyi* were housed in a round basket (30 cm in diameter) placed inside an induced magnetic field (figure 1). The experimental magnetic field was generated by three orthogonal pairs of square Helmholtz coils ( $D=1.5$  m), aligned with the local geomagnetic axis at Beijing (alignment determined using an APS 520 3-axis fluxgate magnetometer with a precision of  $\pm 0.1$   $\mu$ T; Applied

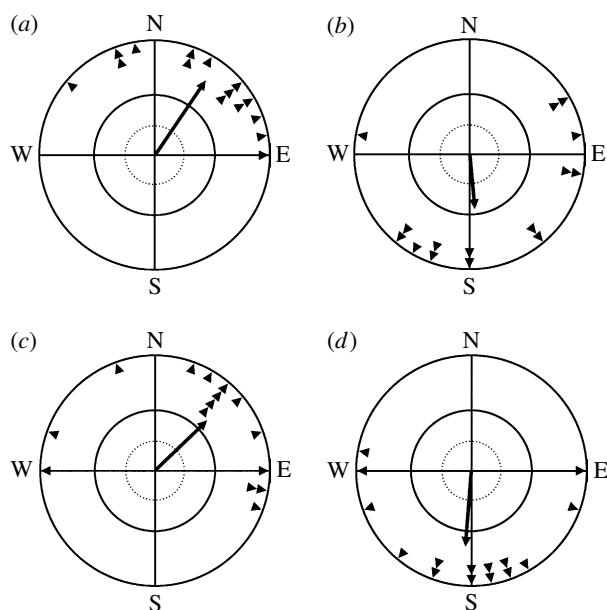


Figure 2. Hanging positions of bats in response to simultaneous changes in the horizontal and vertical components of the altered field. Animals were exposed for 15 days to the normal field (Nm) before the horizontal and vertical components were simultaneously reversed (Nm + H + V). The reversal was done twice giving a total duration of the experiment of 60 days. Symbols at the periphery of the circle indicate the hanging position of the cluster of bats on each night. The arrows represent the mean vector with the length proportional to the radius of the circle = 1. The inner solid and dotted circles represent the 1 and 5% significance level of the Rayleigh test, respectively. The bats always showed a non-random distribution within the basket: (a) Nm: declination =  $1.0^\circ$ , inclination =  $61.3^\circ$  and intensity =  $98.9$   $\mu$ T;  $r=0.78$ ;  $\alpha=33.90^\circ \pm 40.52^\circ$ ,  $p<0.001$ . (b) Nm + H + V: declination =  $183.8^\circ$ , inclination =  $-60.8^\circ$  and intensity =  $100.5$   $\mu$ T;  $r=0.48$ ;  $\alpha=174.66^\circ \pm 69.64^\circ$ ,  $p<0.05$ . (c) Nm: declination =  $359.7^\circ$ , inclination =  $56.1^\circ$  and intensity =  $87.1$   $\mu$ T;  $r=0.62$ ;  $\alpha=46.30^\circ \pm 55.82^\circ$ ,  $p<0.002$ . (d) Nm + H + V: declination =  $181.5^\circ$ , inclination =  $-61.3^\circ$  and intensity =  $98.9$   $\mu$ T;  $r=0.66$ ;  $\alpha=184.52^\circ \pm 52.22^\circ$ ,  $p<0.001$ . When the horizontal and vertical fields were simultaneously reversed, bats changed their roosting positions significantly: (a,b) Watson  $U^2=0.3458$ ,  $p<0.005$ , (b,c) Watson  $U^2=0.3077$ ,  $p<0.005$  and (c,d) Watson  $U^2=0.4636$ ,  $p<0.005$ .

Physics Systems, Mountain View, California), with an intensity twice that of the local field. The roosting position of bats was noted each evening via a remote infrared video camera. Roosting position was defined as the centre of the cluster of roosting bats. When exposed to a normally aligned field (mean declination =  $1.0^\circ \pm 1.4^\circ$ , inclination =  $61.3^\circ \pm 0.9^\circ$  and field intensity =  $98.9 \pm 0.8$   $\mu$ T within the basket) for 15 consecutive days, the bats roosted together at the northern end of the basket (figure 2).

The bats significantly altered their roosting position on the following 15 days after simultaneous changes to the horizontal and vertical components of the field (declination =  $183.8^\circ \pm 1.1^\circ$ , inclination =  $-60.8^\circ \pm 1.3^\circ$ , field intensity =  $100.5 \pm 2.3$   $\mu$ T within the basket). This experiment was then repeated with six different individuals with the same result (see figure 2 legend for statistical results).

To determine whether the bats detected changes in inclination or polarity (or both) of the field, six more bats were exposed to independent changes in the vertical and

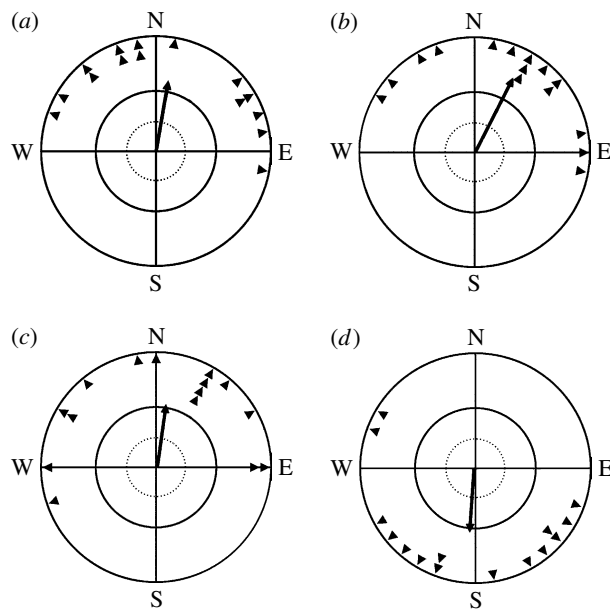


Figure 3. Roosting positions of bats during independent reversals of the vertical and horizontal altered fields. Nm represents the normal field, Nm+H the field after the horizontal field was reversed and Nm+V the field after the vertical field was reversed. Experiments were divided into six parts: normal field in the first 15 days, vertical field reversed in the second 15 days, normal field in the third 15 days and horizontal field reversed in the fourth 15 days. Symbols at the periphery of the circle indicate the hanging position of the cluster of bats on each test night. The arrows represent the mean vector with the length proportional to the radius of the circle = 1. The inner solid and dotted circles represent the 1 and 5% significance level of the Rayleigh test, respectively. Bats always showed a non-random distribution within the basket: (a) Nm: declination =  $359.8^\circ$ , inclination =  $58.5^\circ$  and intensity =  $92.0 \mu\text{T}$ ;  $r = 0.62$ ;  $\alpha = 9.01^\circ \pm 55.97^\circ$ ,  $p < 0.002$ . (b) Nm+H: declination =  $358.8^\circ$ , inclination =  $-64.7^\circ$  and intensity =  $114.6 \mu\text{T}$ ;  $r = 0.71$ ;  $\alpha = 26.20^\circ \pm 47.66^\circ$ ,  $p < 0.001$ . (c) Nm: declination =  $0.1^\circ$ , inclination =  $56.2^\circ$  and intensity =  $88.6 \mu\text{T}$ ;  $r = 0.55$ ;  $\alpha = 7.15^\circ \pm 62.95^\circ$ ,  $p < 0.01$ . (d) Nm+V: declination =  $180.5^\circ$ , inclination =  $61.3^\circ$  and intensity =  $100.8 \mu\text{T}$ ;  $r = 0.55$ ;  $\alpha = 183.03^\circ \pm 62.54^\circ$ ,  $p < 0.01$ . Only when the horizontal field was reversed did the bats significantly change their roosting position: (a,b) Watson  $U^2 = 0.1203$ ,  $p > 0.10$  and (c,d) Watson  $U^2 = 0.3883$ ,  $p < 0.005$ .

horizontal components of the field (figure 3). When exposed to the normally aligned field (declination =  $359.8^\circ \pm 3.6^\circ$ , inclination =  $58.5^\circ \pm 1.9^\circ$  and field intensity =  $92.0 \pm 1.0 \mu\text{T}$  within the basket) for 15 consecutive days, the bats again roosted at the northern end of the basket. When only the vertical component of the field was altered for 15 days (declination =  $358.8^\circ \pm 1.5^\circ$ , inclination =  $-64.7^\circ \pm 1.6^\circ$  and field intensity =  $114.6 \pm 3.2 \mu\text{T}$  within the basket), the bats maintained their roosting position. However, when only the horizontal field was altered for 15 days (declination =  $180.5^\circ \pm 1.8^\circ$ , inclination =  $61.3^\circ \pm 1.2^\circ$  and field intensity =  $100.8 \pm 1.2 \mu\text{T}$  within the basket), the bats significantly altered their roosting position to the southern end of the basket (see figure 3 legend for statistical results).

#### 4. DISCUSSION

Results of our experiments show conclusively that *N. plancyi* reacts to changes in the horizontal component

of an induced magnetic field. We therefore reject our null hypothesis and conclude that *N. plancyi*, unlike all other non-mammalian vertebrates tested to date, reacts to changes in the polarity, but not inclination, of an induced magnetic field. Our experiments also show that magnetic cues are important in the roosting behaviour of *N. plancyi*.

In our experiment, the clear preference for roosting at the northern or southern (normal or reversed) end of the basket suggests a role for magnetic orientation in thermoregulatory behaviour. Species of the genera *Myotis* have been shown to select roosting positions based on their thermal profile, with warmer sites chosen to control the rate of lactation and foetal and juvenile development (Dietz & Kalko 2006; Solick & Barclay 2006). *Myotis* bats have also been shown to select roosting sites that minimize energetic costs of entering, maintaining and leaving daily torpor. Bats also select areas exposed to evening Sun to maximize benefits of solar energy when exiting torpor (Riskin & Pybus 1998; Solick & Barclay 2006).

While not tested directly, our results are consistent with the use of a magnetic polarity-based compass in local navigation (Phillips 1986). Both birds and bats are capable of ranging over long distances while foraging or migrating. For example, *Nyctalus noctula* have been shown to migrate 1600 km between summer and winter roosts (Streikov 1969); Mexican free-tailed bats (*Tadarida brasiliensis*) travel more than 1300 km to their colonies every spring (Villa & Cockrum 1962); the spotted bat (*Euderma maculatum*) can fly for up to 40 km while foraging (Rabe et al. 1998). Magnetic cues have been shown to be used widely by birds and more recently by the big brown bats (*Eptesicus fuscus*; Holland et al. 2006), and it is probable that other species also possess this ability. However, unlike birds, the use of a polarity compass by bats allows them to differentiate between north and south at any point on the Earth, with magnetic intensity possibly providing latitudinal information for precise position determination (Wiltschko & Wiltschko 1996).

The anatomical and physiological mechanisms by which animals detect magnetic information have been investigated for several decades with two competing receptor theories emerging, one based on light and the other on magnetite. Birds and salamanders exhibit correct orientation only when exposed to a narrow wavelength of light while using magnetic information (Phillips & Borland 1994; Wiltschko & Wiltschko 2001), and some birds seem to react during orientation to variations in light intensity (Wiltschko et al. 2000). Magnetite has been found in tissues at the anterior end of the abdomen of honeybees (*Apis mellifera*; Gould et al. 1978), the ethmoid tissue of salmonid fish (Mann et al. 1988), the olfactory lamellae of rainbow trout (*Oncorhynchus mykiss*; Walker et al. 1997) and the orbital and the nasal cavity of birds (Beason & Nichols 1984; Williams & Wild 2001). Model calculations indicate that these magnetite-based receptors may be involved in estimating the direction or intensity of the magnetic field (Wiltschko & Wiltschko 2005). It has even been suggested that birds may use both receptor types with a light-dependent mechanism in the right eye providing directional information and the magnetite-based receptors in the upper beak detecting variation in magnetic intensity (Wiltschko et al. 2002).

Based on bats' relatively (compared with birds) poor eyesight (Altringham 1998) and the low-light conditions



under which they are active, the use of a light-based receptor seems unlikely. Therefore, we hypothesize that bats use a magnetite-based mechanism during orientation. Comparative evidence to support our hypothesis comes from the work which shows that rodents rely on a polarity- and magnetite-based compass under low-light conditions (Marhold *et al.* 1997).

Our work raises questions about the role of the magnetic compass in navigation by bats and possibly other vertebrates. Both the intensity and inclination of the Earth's magnetic field can provide information about latitude (Walker & Bitterman 1989; Wiltschko & Wiltschko 1996). There is now clear evidence that at least some animals are sufficiently sensitive to magnetic intensity to be able to determine latitude (Walker 1998; Dennis *et al.* 2007). If intensity alone is sufficient for determination of latitude, it is reasonable to ask whether polarity and inclination (Wiltschko & Wiltschko 1992) are sufficient for the use of the magnetic compass in the tropics, where bats are abundant and when crossing the magnetic equator during migration. Furthermore, the revelation that a volant mammal possesses and uses a magnetic polarity compass suggests that the ability to detect the axis of the Earth's magnetic field through either polarity or inclination is sufficient for long-distance navigation and raises the possibility that inclination and polarity compasses evolved independently in birds and mammals following the transition from water to land to air.

Care of animals used in experiments was in accordance with guidelines of the Chinese Academy of Sciences.

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